Territorial defense and advertisement by footdrumming in bannertail kangaroo rats (*Dipodomys spectabilis*) at high and low population densities

Jan A. Randall

Biology Department, Central Missouri State University, Warrensburg, Missouri 64093, USA

Summary. Behaviors associated with territorial defense of large dirt mounds by bannertail kangaroo rats (*Dipodomys spectabilis*) at high and low population densities are reported. Rats were observed for 640 h during three summers and one spring from 1980–1982 in SE Arizona.

Bannertail kangaroo rats defended their territories by footdrumming, as a long-distance warning signal, and chasing as a closer-distance threat. They footdrummed on or near their mounds spontaneously during the night, in response to neighbors' footdrums, and during mound challenges. There were no sexual differences in footdrumming, and juveniles frequently performed the behavior. The low frequency sounds were within the auditory sensitivities of the rats and footdrumming patterns differed somewhat between individuals. A playback experiment provided preliminary evidence that rats can differentiate between the footdrums of neighbors and strangers. When a bannertail visited the mound of another bannertail the mound owner actively defended its mound and immediately chased the visitor away. Fighting and mound challenges occurred infrequently, and the uniformly dispersed distribution of mounds suggested an effort by rats to avoid mutual interference.

When population densities were high, dispersing juveniles built new mounds, consequently, distances between mounds decreased. Rats responded by tolerating closer neighbors, spending more time active on their mounds, and visiting neighboring mounds less. Adults increased footdrumming rates at high population densities, but juveniles footdrummed at high rates regardless of the population size.

Introduction

The bannertail kangaroot rat (*Dipodomys spectabilis*) spends most of its active time on large, conspicuous dirt mounds that can be up to 5 m in diameter and 0.5 m high (Holdenried 1957; Schroder and Geluso 1975). Each mound is inhabited by an adult male or female, and an animal may have more than one mound in its home area. Since some juveniles are born in late winter and reach adult size and disperse by early summer (Holdenried 1957), juvenile rats also inhabit and defend mounds during most of the year.

The generally small home areas of *D. spectabilis* overlap very little (Schroder 1979). On average, a rat spends most of its active time inside or on the mound and only a small percentage of time more than 6 m away from the mound. Rats store as much as 100 l or more of seeds in a mound and possibly exceed all other animal species in this activity (Monson 1943). Mounds are considered too large and elaborate for a single animal to build and often represent the efforts of successive generations of kangaroo rats (Best 1972; Holdenried 1957; Vorhies and Taylor 1922). Because the area surrounding the mound is rich in seed resources, and the mound and its seed cache seem essential for survival and reproduction (Best 1972; Holdenried 1957; Schroder 1979), the energy expenditure required for territorial defense appears worthwhile (see Davies 1978).

Bannertail kangaroo rats advertise their presence on the mound by footdrumming. Footdrumming in rodents has been reported in a number of different contexts, but the functional signifi-

cance of this behavior has not been studied in detail in any species. Eisenberg (1963) described it in five species of kangaroo rats, but he was unable to assign a function. Several species footdrum during or after mating, including *Dipodomys microps* (Kenagy 1976) and gerbil species (Burley 1980; Dewsbury 1971; Dewsbury et al. 1978; Holman and Hutchison 1982; McDermott and Carter 1980; McDermott et al. 1980). Ground squirrels and prairie dogs footdrum defensively at snakes (Coss and Owings 1978; Owings and Owings 1979; Richardson 1942), and the behavior also has been associated with escape and hiding (Clark and Galef 1977, 1979; Eisenberg 1963) and agonistic interactions (Ferron 1979; Howe 1978).

The spatial organization and behavior of *D. spectabilis* fulfill the criteria for a territorial system (Brown and Orians 1970; Waser and Wiley 1979): rats restrict some or all of their activities to an area, maintain exclusive possession of it, and advertise their presence in it. In this paper, I detail the behaviors associated with territorial defense and footdrumming in the bannertail kangaroo rat. I also provide information on differences in territorial organization and defense at high and low population densities.

Materials and methods

The study area. A 120 × 120 m (1.44 ha) study plot was established in June 1980 about 7 km east of Portal, Arizona. This area was expanded to 150 × 150 (2.25 ha) in March 1981 to increase the sample size of animals available for observation, especially *Dipodomys merriami*, since about one-half of the site consisted of *D. spectabilis* habitat and the other half *D. merriami* habitat, which tended to be brushier. Numbered stakes were placed every 15 m to aid in live-trapping and animal census, and the bannertail mounds were identified and numbered. Distribution of mounds on the study area was determined by measuring distances between the bases of all mounds on the study site.

Animal identification. Resident rats were live-trapped and marked with color coded ear tags that were covered with luminescent colored tape (Scotchlite) for individual identification at night. Black dye marks at different locations on an animal's body also helped to identify frequently observed animals. The study area was periodically trapped to census animals, replace tags, mark untagged animals, and to weigh, measure foot lengths, and record reproductive condition. Mound residency was censused by periodically trapping or spotlighting animals on their mounds.

Observations. Observations occurred at night, usually from sunset to 0200–0400 h, depending on weather and rat activity. Windy nights greatly reduced rat activity, but moonlight seemed to have no consistent influences, and rats exhibited a great deal of individual variation in activity patterns. I attempted to systematically observe all occupied mounds on the study area, but because of the variables mentioned above, some ani-

mals were observed much more frequently than others. I usually observed one bannertail mound in a night or surveyed the study area and recorded behaviors. A few mounds were close enough together, especially in 1982, so that I could see more than one mound at a time. To observe a bannertail mound, I hung two lanterns from 2 m high metal tripods and positioned them so that they cast a dim light on the mound. Rats were observed with binoculars from a 1 m high platform at least 15 m away from the mound behind the lights; many rats favored one side of the mound so the platform was positioned accordingly. I could usually see an area of about 5 to 8 m around the mound. Most rats habituated readily to the lights and my presence. A small amount of seeds was scattered on a mound at the beginning of each observation period to entice the mound owner out for identification. This may have influenced frequencies of animal interactions; however, effects were probably consistent through the study period.

I observed bannertail mounds for a total of 640 h from 16 June to 19 August 1980 (215 h), 30 March to 9 May (110 h) and 14 July to 6 August (70 h) 1981, and 15 May to 13 September 1982 (245 h). Additional hours were spent surveying the study area. All observations were recorded by speaking quietly into a hand-held tape recorder. The following observations were recorded: (1) all approaches, chases, fighting, and relationships between mound owners and intruders, (2) frequency and context of and responses to footrolls (a footroll consisted of a continuous series of footdrums; a footdrum resulted from hitting one or both hind feet on the ground.), (3) the amount of time spent inside and outside the mound, and (4) locations of animals when engaged in behaviors.

Playback experiment. Responses of ten kangaroo rats to audio playbacks of footdrumming recordings of neighbors, strangers (unfamiliar rats), and their own were tabulated from 2 to 16 August 1982. Cricket stridulations, recorded on the study site, served as a control. Recordings of airborne footdrumming sounds of neighbors and an animal's own were obtained with a Uher 4000 tape recorder at a tape speed of 9.5 cm/s between 17 and 26 July 1982 from about 0100 to 0400 hours by placing an omni-directional microphone (Sennheiser ME 80) into a burrow entrance after an identified rat was observed entering and heard footdrumming. In-mound drummings were used to avoid extraneous noises, especially wind and insect sounds, and because of the difficulty in recording long durations of footdrummings on the mound; rats tended to cease drumming and run into the mound upon seeing me nearby. In-mound recordings sounded similar to, but slightly more muffled than, sounds recorded on the mound. Sound spectrograms of in-mound and on-mound recordings appeared similar, and the temporal patterns of the sounds remained the same. Recordings of footdrums of three unfamiliar rats were obtained similarly from animals from an area 4 km away on 26 July 1982.

A speaker was hidden in vegetation 2 m from the edge of a test animal's mound on the same side as the neighbor whose recordings were to be played. Playbacks from the Uher recorder were controlled by me on an observation platform at least 15 m away. Each test consisted of 10 min pre-playback period, 5 min of playback, and 10 min post-playback observations so that at least 30 min elapsed between tests. Playbacks began after dark when the test subject had emerged from its burrow and been active at least 10 min. A handful of seeds was sprinkled on the mound to increase surface activity. One animal was tested per night in a counterbalanced design to control for sequence effects. I recorded the amount of time within 2 m of the speaker, approaches to the speaker, and frequency of footdrumming in response to the playback recordings.

Acoustic analysis. A Kay (6061) Sound Spectrograph, narrow band (45 Hz filter in the 80 to 8,000 Hz range), was used to make sound spectograms of footdrumming frequencies of a juvenile male rat recorded on his mound at 0200, 21 July 1982, with a Uher 4000 recorder at a tape speed of 9,5 cm/s and an omni-directional microphone. I used a Tektronix R5103N Oscilloscope and Nihon-Kohden camera to produce oscillograms of footdrumming patterns of animals that I recorded for the playback experiment.

Data analyses. Data were combined across season and years as specified, and footdrumming rates were expressed as the number of footrolls/h of individual rat activity. A minimum of 3 h of activity was tabulated for each rat used in data comparisons. Footdrumming data from 1980 and 1982 were compared because of larger sample sizes, similar numbers of hours of observation, and less overlap of data for the same animals. Data for the summer of 1981 were limited because of fewer total hours of observation and animal inactivity. I combined data across years without regard to population density to gain adequate sample sizes for statistical comparisons of general footdrumming rates of males and females and juveniles and adults. Combining data did not appear to confound the results. A G-test of independence, using Williams correction, Mann-Whitney U-test, χ^2 tests, and paired t-test were used where appropriate. I normalized data from the playback experiment with a log transformation to meet the assumptions for an analysis of variance (Sokal and Rohlf 1981). I then analyzed them with a repeated measures, single classification, analysis of variance and a Student Newman-Keuls as a posteriori test (Keppel 1973).

Results

Population densities

Populations on the study site remained relatively stable in 1980 and 1981. There were 12 residents in the summer of 1980 and 16 in the spring and 14 in the summer of 1981. Numbers of juveniles and adults occupying territories in the summers of those years were similar: five adults and seven juveniles and eight adults and six juveniles, respectively. In spring 1981 adults predominated, since most juveniles had not begun to disperse, and 12 adults and four juveniles defended mounds. Eleven of 12 animals stayed from August 1980 to March 1981, and in August 1981 eight of the original animals from 1980 were still present.

Populations more than doubled in 1982, as reflected by the number of occupied and newly built mounds (Fig. 1). The population consisted of 12 adults and 25 juveniles, with 9 adults remaining from the previous year. Whereas four animals in 1980 and three in 1981 occupied more than one mound, in 1982 all animals were restricted to only one mound. Rats inhabited all unoccupied mounds from previous years, and juveniles constructed 11 new ones during the course of the summer. Construction of mounds had never been observed in
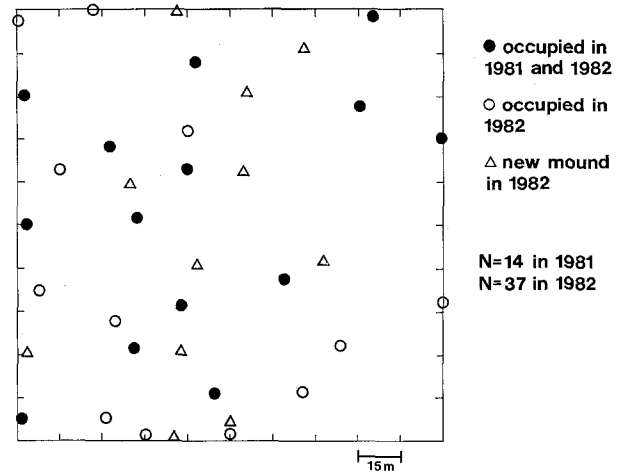

Fig. 1. Spatial distribution of occupied *D. spectabilis* mounds on a 2.25 ha area in high (1982) and low (1981) population densities. *Closed circles* indicate mounds occupied in both 1981 and 1982; *open circles* represent mounds not occupied in 1981 but occupied in 1982; and mounds designated with a *triangle* were new mounds built in 1982

prior years. Most of the new mounds were dug out from underneath *Ephedra* and mesquite (*Prosopis*) bushes, and bannertails began to take over *D. merriami* burrows as they encroached into their area. I observed one bannertail dig in a *D. merriami* burrow, chase out the owner, excavate the mound, and subsequently defend the territory.

Distances between closest neighbors on the study site were almost identical in 1980 (27.8±4.8 m) ($\bar{x}$±SD) and in 1981 (27.2±7.8 m). As a result of increased densities, however, distances between inhabited mounds on the study area decreased significantly from 1981 to 1982 (Fig. 1). The closest neighbor in 1981 averaged 27.2±7.8 m compared to 15.8±8.3 m for the same 14 mounds in 1982 ($P<0.001$, $t=5.09$, $df=13$, paired t-test). The farthest neighbor was 56.9±7.5 m in 1981 compared to 42.5±7.1 m in 1982 ($P<0.01$, 3.67, $df=13$). The average number of neighbors increased from 4.5±1.8 to 6.1±1.1 ($P<0.01$, $t=3.22$, $df=13$). An unusual example of neighbor proximity was occupancy of opposite ends of the same mound by an adult male and juvenile female. After several weeks, the adult male displaced an adult male in an adjacent mound, leaving the female in the original one.

A nearest-neighbor analysis revealed that mounds were distributed in a non-random, dispersed fashion at both high and low population densities (Clark and Evans 1954). The mean distance between nearest neighbors of the 12 occupied mounds in 1980 was 27.8 m with an expected value
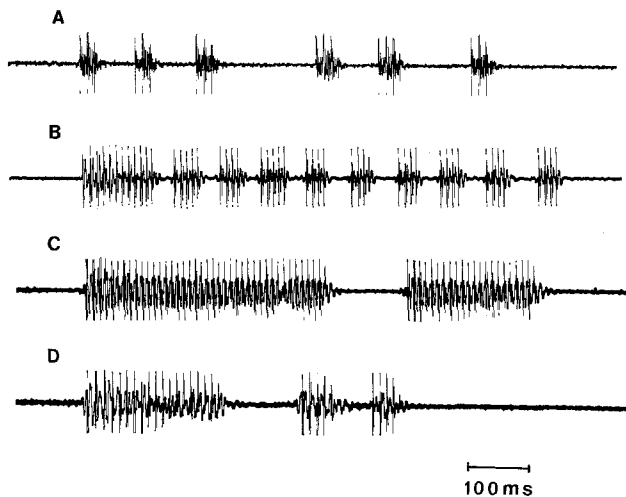
Fig. 2. Osillograms of footdrumming patterns of an adult male (A), adult female (B), and two juvenile females (C, D). The footdrummings were of territorial neighbors recorded 22 July 1982 between 0200 and 0400 hours and used in playback experiments

Fig. 3. Sound spectogram of a bannertail footdrum

of 17.3 m to yield a R value of 1.6 ($R > 1$ indicates a non-random, uniform distribution). Of the 14 occupied mounds in 1981, the expected distance was 20.1 m compared to 27.2 m to yield a R value of 1.4. The mean distance between nearest neighbors of the 37 mounds on the study area in 1982 was 14.5 m with an expected distance of 12.3 m; a R value of 1.2 was found.

Footdrumming

Charactristics of footdrumming. Each time a rat's feet strike the substrate constitutes a footdrum. A continuous series of footdrums is a footroll, and several footrolls in a series comprise a footdrumming sequence (Fig. 2). The characteristics and consistency across time of footdrumming patterns of different animals are currently being analyzed. Preliminary results show that rats usually produce several footrolls in a sequence ($\bar{x} = 5.3 \pm 4.2$) ($\bar{x} \pm$ SD, $n = 486$ footrolls from 15 animals), and the number of drums per footroll and footrolls in a sequence vary among some individuals (Fig. 2).

Sound spectrograms revealed that most of the energy in footdrumming sounds occurs at frequencies less than 2000 Hz (Fig. 3).

Location. During their activity periods, kangaroo rats footdrummed spontaneously in 62.9% of all footrolls counted ($n = 39$ animals, 6949 total footrolls), in response to neighbors' footdrums (20.6%), and during mound challenges (16.5%).
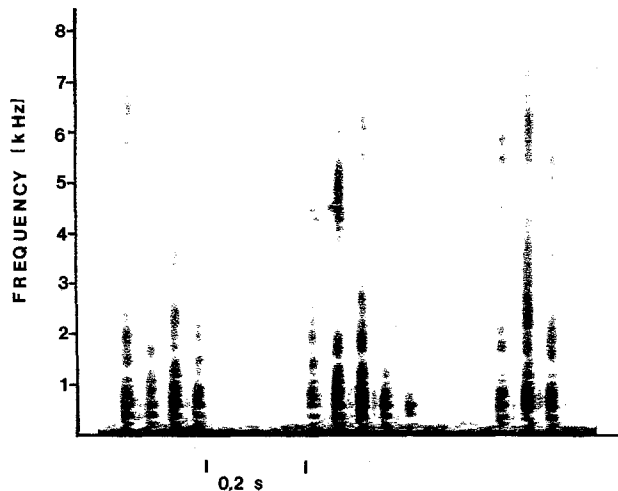
On average a rat spent 5% of its observed activity footdrumming in the vicinity of the mound. Ninety-four percent of all footrolls by mound owners in all contexts in which location could be tabulated ($n = 31$ animals, 4314 footrolls) in 1980 and 1982 occurred on, inside, or at the base of the mound with the majority on the mound. Only 6% of the footdrumming was more than 2 m from the mound ($G = 227$, $df = 3$, $P < 0.001$). No differences in footdrumming location occurred between years. Drumming rates on the mound may be somewhat inflated, however, since I observed rats primarily in the vicinity of the mound.

Sex and age differences. I found no sex differences in footdrumming rates (combined spontaneous footdrumming rates and rates of drumming in response to neighbors' footdrums across years for animals observed active at least 3 h). Adult males averaged 6.69 ± 5.36 ($\bar{x} \pm$ SD) footrolls/h of activity ($n = 7$) compared to 4.81 ± 6.14 for adult females ($n = 7$) (NS, Mann-Whitney U-test). Juvenile males and females also showed no differences in footdrumming rates. Juvenile males averaged 23.95 ± 18.7 footrolls/h of activity ($n = 7$), while juvenile females averaged 19.94 ± 15.24 ($n = 10$). Juveniles, however, footdrummed at significantly higher rates than adults ($P < 0.05$ for comparisons between adult and juvenile males and adult and juvenile females respectively). Juveniles averaged 21.42 ± 16.7 footrolls/h of activity compared to only 5.75 ± 5.62 for adults (data for males and females combined, $P < 0.01$).
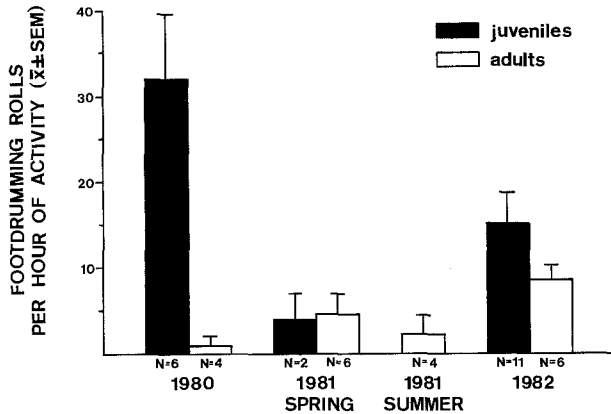
Fig. 4. Rates of footdrumming by adult and juvenile *D. specta-bilis* in low (1980, 1981) and high (1982) population densities
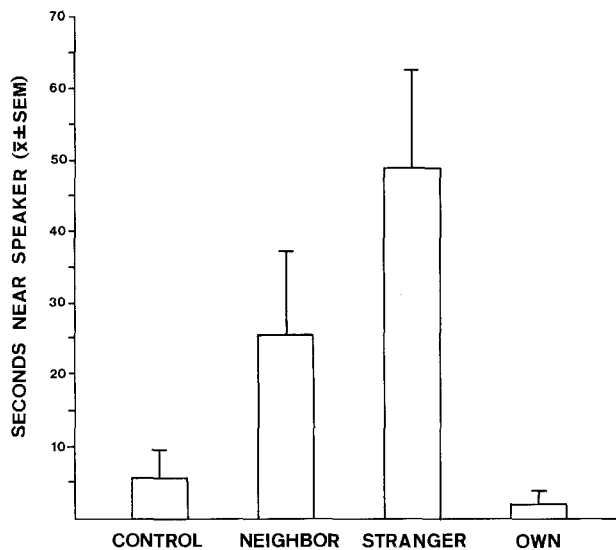

Fig. 5. Responses of rats to footdrumming recordings of neighbors, strangers, their own, and cricket stridulation as a control during the playback and post-playback observation period ($n=$ 10)

Density effects. When footdrumming rates were compared for juveniles and adults within years, juveniles footdrummed at significantly higher rates than adults in 1980, a low density year ($P<0.01$, Mann-Whitney U-test) (Fig. 4). Juveniles exhibited higher footdrumming rates than adults in a high density year (1982), but the data were not significant because adult rates had increased. Footdrumming rates of adults were significantly higher in 1982 than in the summers of 1980 ($P<0.01$) and 1981 ($P<0.05$), both low density years. No significant differences were found for comparisons of adult footdrumming rates for spring 1981 and the three summers. (I could not compare adult and

juvenile footdrumming rates in 1981 because of insufficient data for juveniles.)

Playback experiments. The amounts of time spent within 2 m of the speaker during the playback and post-playback periods were compared (Fig. 5). Rats spent significantly more time within 2 m of the speaker in response to the footdrummings of a stranger than to those of a neighbor ($P<0.05$). They also spent more time near the speaker in response to the footdrummings of a stranger ($P<0.01$) and a neighbor ($P<0.01$) than to the control and in response to the footdrummings of a stranger ($P<0.01$) and a neighbor ($P<0.05$) than to their own footdrummings.

Nine of ten rats exhibited a response to the playback recordings of the stranger by either approaching the speaker or by approaching and footdrumming in return. Five rats footdrummed in response to the footdrums of a stranger compared to five not footdrumming. Five of ten rats approached the speaker in response to playbacks of footdrums of a neighbor, and three footdrummed in response. Only one rat responded to the playback of its own footdrumming by approaching the speaker, but three footdrummed in response.

Mound defense

Bannertail kangaroo rats actively defended their mounds from all intruders. I observed chasing in 62% of the 147 visits of intruders to the mounds of other bannertails, and I documented only 11 body contacts and five brief roll-over fights. Fourteen percent of the visitors left upon seeing the owner before a chase, and 24% left before they were detected by the mound owner. During a chase, a mound owner leaped into the air and rushed toward a visitor, thus causing its immediate departure. Intruders were either on the mound or at its base by the time a chase began (95% of chases). Owners chased intruders an average distance of 7.5 ± 6.2 m ($\bar{x} \pm$ SD) from the mound and then quickly returned to resume foraging or to enter the mound.

The majority of visitors were neighbors that quickly returned to their own mounds when chased (Table 1). Of the 147 visits, 14% were by untagged animals that were probably dispersing. The remainder were ear-tagged juveniles attempting to return to their natal mounds after being chased away by their mothers. Juveniles and adults visited at similar rates during the summers, but in the spring, 89% of all identified visitors (65 of 73

Table 1. Number of visits by neighbors, dispersing rats, and returning juveniles to occupied mounds during summers of 1980–1982 and spring of 1981. Weighted totals are based on the longest observation time (245 h)

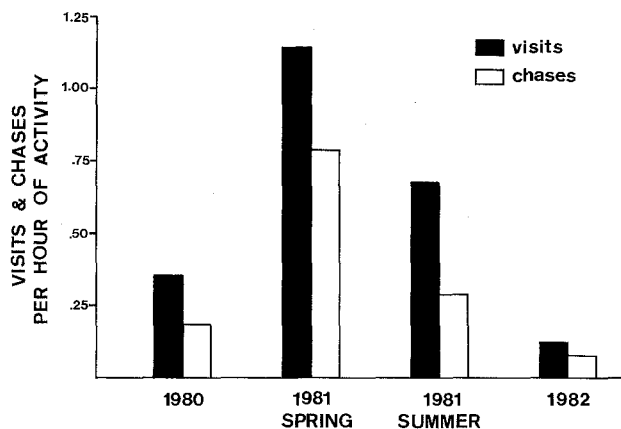|	Neighbors	Dispersers	Returning juvenile(s)	Total	Time observed (h)	Totals weighted for h of observation
1980	24	4	4	32	215	36
1981 (spring)	62	9	2	73	110	163
1981	16	0	1	17	70	59
1982	17	8	?	25	245	25
Total	119 (81%)	21 (14%)	7 (5%)	147 (100%)	640	283

Fig. 6. Rate of visits by *D. spectabilis* to occupied mounds and rate of chases by mound owners during three summers (1980–1982) and one spring (1981)

visits) were adults. Of these, 67% of visits were by adult males to mounds of adult females, 19% adult females to adult females, 10% adult males to adult males, and 4% by adult females to adult males and to juveniles.

Rates of visiting and chasing varied according to season and population density (Fig. 6). Rats visited less than expectd at high population densities in 1982 and more than expected in the spring when densities were lower ($\chi^2_3 = 105.9$, $P < 0.001$; goodness-of-fit test of rates of visiting across years and season, Lehner 1979). Similar results were found for chases ($\chi^2_3 = 78.09$, $P < 0.001$).

Rats also spent more time on their mounds when population densities were high. Of 245 total hours of observation in 1982, rats were active 69% of the time as compared to 42% and 36% in the summers of 1980 and 1981, respectively. Rats were active 60% of the observation time in the spring of 1981 and visited at rates higher than expected. Rats visited less then expected for the number of

hours of activity in 1982 ($\chi^2_3 = 66.16$, $P < 0.001$; test of association of visits and activity across season and years).

Mound challenges

Five visits of bannertail kangaroo rats to mounds of conspecifics resulted in challenges. Ear-tagged neighbors represented two of the challengers, and three were probably dispersing juveniles. Three of five challenges occurred in 1982 when densities were high.

A challenge began when a rat visited a mound and continued to approach after being chased by the resident. The frequency of chasing and approaching by the mound owner and challenger depended on mound ownership: the owner chased the challenger in 34 of 35 chases and approached twice, and the challenger approached the mound 37 of 39 times and chased once ($G = 35.8$, $df = 1$, $P < 0.001$). Footdrumming contests were interspersed between approaches and chases and occurred when animals stood a few meters apart, faced each other, and footdrummed until, with one exception, the owner rushed and chased the challenger. Challenges lasted from 0.53 to 3.65 h with one to seven footdrumming contests per challenge. Each footdrumming contest continued for 0.25–4 min, and there was only one brief fight during the five challenges. Four of five challenges were instigated by juveniles, but all mound owners, three adults and two juveniles, retained ownership of their mounds at the time of the challenge.

The highest rates of footdrumming occurred during mound challenges, and both the challenger and mound owner footdrummed at similar rates. The challenger averaged 135.8 ± 180 footrolls/h ($\bar{x} \pm SD$) compared to the resident's 123.6 ± 69 (NS, Mann-Whitney U-test). Rats participating in the challenges averaged 129.7 ± 129 ($n = 10$) foot-

rolls/h compared to a general rate of spontaneous footdrumming of 8.15 ± 5.2 footrolls/h ($n = 31$ juvenile and adult males and females combined across years ($P < 0.01$).

Discussion

The social organization of *D. spectabilis* remained relatively stable during the study. Rates of survival and carry-over of residents from year to year were fairly high, and animals defended and retained their territories. Although intruders encroached upon the territories of others, agonistic behaviors were restricted to chasing. Fighting occurred rarely, and mound challenges happened infrequently, even at high population densities. Most of the visitors to mounds were neighbors who had their own territories and probably represented little threat. Time and energy spent on territorial defense seemed devoted to footdrumming, as a long-distance warning signal, and to chasing as a closer distance threat.

Effect of population density on territorial defense

Construction of 11 new mounds by juveniles on the study area in 1982 was highly unusual and reflected total mound saturation because of extremely high population densities. Studies of *D. spectabilis* indicate that building new mounds is a slow, rarely observed process. Juvenile *D. spectabilis* usually reinhabit existing mounds, even if they are old and collapsed, rather than build new ones (Best 1972; Holdenried 1957; Schroder 1979). Because populations of dispersing juveniles in 1982 greatly exceeded availability of mounds, including damaged ones, rats were forced to either build new ones or to challenge mound owners. Rather than challenge mound owners, dispersing rats built new ones. Whether the new mounds afforded the same survival value as ones that were already established cannot be ascertained, but the new mounds appeared small and shallow and probably offered temporary space for survival until a better territory became available.

Remaining close to the mound at high population densities was probably the best territorial defense. Rats visited less than expected at high densities, spent more time active on their mounds, and advertised their presence by footdrumming. Because mounds were limited and animals without mounds present, a mound was a resource in high demand and an owner might have much to lose if it left it for even a short time to visit a neighbor.

Ownership itself affords an advantage to territorial owners (Davies 1978; Parker and Rubenstein 1981), but animals must be present to defend their territories against dispersing animals.

The generally uniform distribution of mounds in both high and low population densities suggested an effort by kangaroo rats to avoid mutual interference. Although distribution patterns were similar in 1980, 1981, and 1982, more mounds were packed into the study area when population densities were high. Rats tolerated neighbors at much closer distances in 1982 than in previous years, and the sharing of a mound by two animals seemed quite unusual. Some rats probably could chase away close neighbors, but even if successful, a new rat would soon attempt to move into the vacant mound, requiring too much time and energy to maintain the vacant space. A better strategy was for a rat to decrease its "aggressive field" and to avoid neighbors living in close proximity (Waser and Wiley 1979). Aggressive fields may have changed in the fall, however, when rats began to harvest seeds.

Footdrumming

Footdrumming seems an important aspect of territorial defense in *D. spectabilis*. The footdrumming of rats to signal ownership of mounds parallels that of song birds singing to advertise a territory. In both song birds and kangaroo rats, the use of long-range, persistent signals, rather than physical contact, greatly reduces risk of injury and the energy required for territorial defense (Davies 1978; Waser and Wiley 1979).

Bannertail kangaroo rats footdrum on their mounds to signal acoustically their location. The distance that footdrumming sounds transmit is unknown. However, since rats footdrum in response to neighbors' drumming, they probably can hear from mound to mound, at least 16 to 27 m depending on population densities. I could hear footdrumming at these distances on a windless night. Rats seemed reluctant to footdrum away from the mound, and I often observed them run to a vantage point on top of their mounds to drum. Because mounds were hollow as a result of burrow excavations, rats may footdrum from the top to maximize sound transmissions.

The high degree of correspondence between auditory sensitivity of kangaroo rat hearing and the frequency range of footdrums supports the hypothesis that rats hear footdrumming at relatively long distances. Kangaroo rats possess greatly inflated middle ears and acute sensitivity to low-fre-

quency sounds; peak sensitivity of hearing is approximately 1000 Hz (Webster 1962; Webster and Webster 1980). Sound spectograms of footdrumming recordings show that most of the energy in footdrumming sounds occurs at frequencies of between 200 and 2000 Hz. Low-frequency sounds attenuate slowly and carry further distances than high-frequency sounds (Gould 1983). Sensitivity of kangaroo rats to low-frequency sounds has been interpreted as an adaptation for predator avoidance in open habitats and not as an adaptation for conspecific communication (Webster 1962; Webster and Webster 1980). My data suggest, however, that *D. spectabilis* hears well at low frequencies as an adaptation for conspecific communication.

The playback experiment provides preliminary data that territorial rats respond with different intensities to footdrums of different individuals, and they may distinguish between familiar footdrums of neighbors and unfamiliar footdrums of strangers. Neighbor-stranger discrimination also has been demonstrated experimentally in numerous species of song birds (see Beletsky 1983 for a review). The ability to distinguish between familiar and unfamiliar conspecifics enables territorial owners to determine whether a footdrummer is an established neighbor and little threat or an unsettled transient searching for a territory and thus a threat (Waser and Wiley 1979). Rats probably recognize neighbors as a class of familiar footdrumming patterns versus unfamiliar ones rather than by recognition of individual patterns. While oscillograms illustrate that footdrumming patterns of some animals differ distinctively, oscillograms of others show pattern similarities (Randall, unpublished data). The extent of overlap of individual patterns is being investigated, and at present, individual recognition by footdrumming in *D. spectabilis* has not been demonstrated.

Some characteristics of footdrumming in *D. spectabilis* differ from auditory communication in many birds and some mammals (Gould 1983). For instance, males and females exhibit similar footdrumming behaviors, but in birds territorial defense is often only associated with males (Beletsky 1983). Secondly, juveniles footdrum at even higher rates than adults. Footdrumming seems especially important for the establishment of territories by juveniles. They even footdrum at high frequencies in low population densities when extra mounds are available. Juveniles reach adult size within a few months after birth in the late spring and during the summer (Holdenried 1957), and they must obtain a mound and fill it with seeds in the fall for successful reproduction the following spring. After

establishment of territories, footdrumming rates of adults are lower than those of juveniles, but adult rates increase if population size increases. As density increases, neighbors are closer and the probability of encounters greater. Many species increase frequencies of threat and avoidance as distances between conspecifics decrease (Waser and Wiley 1979).

Seasonal variations

D. spectabilis ventured farther from their mounds and took more excursions in the spring than in the summer months; however, Schroder (1979) found no significant change in seasonal activity patterns. Besides observing more visits to mounds, I also trapped and observed rats farther away from their territories in the spring. Two factors could account for the increased movement. Rats gather seeds during the spring and fall after seeds drop from winter and summer annuals, respectively, (Monson and Kessler 1940; Vorhies and Taylor 1922), so they may venture longer distances in search of seeds. However, fall is the primary season of seed harvest (T. Jones, personal communication). Also, the bannertails reproduce from February through June with the peak in late February to March (Holdenried 1957). Males might leave territories to seek estrous females, as a majority of the visitors in the spring were adult males to the mounds of adult females. Since reproduction occurs at the female's mound (Randall, unpublished observations), males may routinely investigate female territories for olfactory signals indicating estrus.

Social organization

In comparison to other rodents, the social organization of *D. spectabilis* parallels that of arboreal sciurids and chipmunks. Males and females defend territories throughout the year, advertise territories with acoustic signals, and defend their territories by chasing and calling (Elliott 1978; Smith 1968). Social organization of the bannertail differs from the female-based units of many other rodent species such as ground dwelling sciurids (Michener 1983), and the individual female territories with overlapping male ranges found in some *Microtus* (Madison 1980; Redfield et al. 1978) and in *D. merriami* (O'Farrell 1980; Randall, unpublished data).

The evolution of territorial defense requires that individuals obtain some reproductive benefit as a result of access to limited resources (Brown

1964; Davies 1978). Food and mounds are critical resources for reproduction and dispersal in *D. spectabilis* (Brown et al. 1979; Schroder 1979). The ability of bannertails to gain and to hold mounds and their interactions and communication with neighbors determine proximity of conspecifics. The mound provides a base of operation from which rats can enter into familiar areas to forage for seeds and still avoid interference with other kangaroo rats. The spacing of *D. spectabilis* is, therefore, an area large enough to supply adequate seeds and small enough to defend, especially during the fall when rats harvest seeds. Spacing patterns and behaviors, however, can change as ecological variables change. The decrease in territory size and increase in tolerance of neighbors at high population densities demonstrate this in the bannertails. Predictions of spacing are often difficult because complex interactions must be understood in order to determine optimal spacing and activity for a species (Waser and Wiley 1979).

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